Genome-Wide Linkage Analysis to Identify Chromosomal Regions Affecting Phenotypic Traits in the Chicken. I. Growth and Average Daily Gain[1]

H. Zhou,*[2] N. Deeb,* C. M. Evock-Clover,† C. M. Ashwell,†[3] and S. J. Lamont*[4]

*Department of Animal Science, Iowa State University, Ames 50011; and †Growth Biology Laboratory, Livestock and Poultry Sciences Institute, USDA-ARS, Beltsville, MD 20705

ABSTRACT A genome scan was used to detect chromosomal regions and QTL that control quantitative traits of economic importance in chickens. Two unique F_2 crosses generated from a commercial broiler male line and 2 genetically distinct inbred lines (Leghorn and Fayoumi) were used to identify QTL affecting BW and daily average gain traits in chickens. Body weight at 2, 4, 6, and 8 wk was measured in the 2 F_2 crosses. Birds were genotyped for 269 microsatellite markers across the entire genome. Linkage distance among microsatellite markers was estimated by the CRIMAP program. The program QTL Express was used for QTL detection. Significance levels were obtained using the permutation test. For the 8 traits, a total of 18 and 13 significant QTL were detected at a 1% chromosome-wise significance level, of which 17 and 10 were significant at the 5% genome-wise level for the broiler-Leghorn cross and broiler-Fayoumi cross, respectively. Highly correlated growth traits showed similar QTL profiles within each cross but different QTL profiles between the 2 crosses. Most QTL for growth traits in the current study were detected in Gga 1, 2, 4, 7, and 14 for the broiler-Leghorn cross and Gga 1, 2, 4, 5, 8, and 13 for the broiler-Fayoumi cross. Potential candidate genes within the QTL region for growth traits at 1% chromosome-wise significance level were discussed. The results in the current study lay the foundations for fine mapping these traits in the advanced intercross lines and provide a start point for identification causative genes responsible for growth traits in chickens.

Key words: genome scan, quantitative trait loci, growth trait, broiler, inbred line

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INTRODUCTION

The development of molecular biology techniques for uncovering genetic variation at the DNA level has opened new avenues to identify genes affecting quantitative traits. Comprehensive genetic linkage maps for the chicken have been developed over the last decade with an international mapping effort (Bumstead and Palyga, 1992; Crittenden et al., 1993; Groenen et al., 1998; Wallis et al., 2004; Wong et al., 2004).

Quantitative genetic variation is caused by intrapopulation and interpopulation differences for many traits of biological, medical, and agricultural importance (Sewalem et al., 2002). Dissection of the genetic architecture of complex traits in livestock could greatly advance our general understanding of biology and physiology of quantitative phenotypic variation observed in the population (Rocha et al., 2004). The identification and utilization of QTL provide the potential for more rapid genetic improvement in selection programs, especially for traits that are difficult to improve with traditional selection (Ikeobi et al., 2002). Van der Beek and van Arendonk (1996) indicated additional selection responses of 6 to 13% using MAS by incorporating a marker-linked QTL in a simulation study after 5 generations of selection. With detection of large effects on phenotypic traits and the origin of potentially beneficial alleles, the introgression of favorable alleles into commercial lines, or increasing the frequency of desirable alleles, would become feasible in the poultry industry.

Based on chicken linkage maps and data from a variety of populations, several studies have reported the discovery of QTL for BW in chickens. A whole genome scan for QTL affecting BW and growth in a 3-generation population generated from 2 broiler lines was conducted (van Kaam et al., 1998, 1999). Tatsuda and Fujinaka (2001) reported QTL for growth in a F_2 population based on crosses between fast- and slow-growing lines. The QTL affecting early growth in chickens were discovered in a F_2 cross between Red Jungle Fowl and layers (Carlborg et al., 2003), between 2 commercial broiler lines (de Kon-

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[2]Present address: Department of Poultry Science, Texas A&M University, College Station, TX 77843.
[3]Present address: Department of Poultry Science, North Carolina State University, Raleigh 27695.
[4]Corresponding author: sjlamont@iastate.edu

ing et al., 2003; Zhu et al., 2003), between 2 egg-layer lines (Tuiskula-Haavisto et al., 2002), between the White Leghorn and Rhode Island Red breeds (Sasaki et al., 2004), between 2 outcrossed White Plymouth Rock broiler dam lines (Jennen et al., 2004), between 2 layer lines divergently selected for primary antibody response to sheep red blood cell (Siwek et al., 2004), and a F_2 population between Cobb-Cobb broilers and Hy-Line White Leghorn lines (Schreiweis et al., 2005).

Different QTL effects and positions affecting chicken BW and growth were detected in different populations, due to the different lines analyzed and the nature of the quantitative traits. The resource populations used in the current study were generated by crossing 1 modern broiler sire line with 2 unrelated highly inbred lines (Leghorn and Fayoumi lines; Zhou and Lamont, 1999). The unique population design not only maximizes the power to detect linkage disequilibrium, because of the diverse crosses, but also offers the opportunity to identify modulation of QTL effects caused by different genetic backgrounds. Results for BW and growth are presented in this paper; results for body composition traits are presented in companion papers (Zhou et al., 2006). The primary objective of the present study was to detect and localize QTL affecting BW and growth traits in the F_2 population.

MATERIALS AND METHODS

Resource Populations

The Iowa Growth and Composition Resource Population (**IGCRP**) was established by crossing sires from a broiler breeder male line with dams from genetically distinct, highly inbred (>99%) chicken lines, the Leghorn G-B2 and Fayoumi M15.2 (Zhou and Lamont, 1999; Deeb and Lamont, 2002). The F_1 birds were intercrossed, within dam line, to produce 2 related F_2 populations. Birds (n = 417 in broiler by Leghorn cross, n = 325 in broiler by Fayoumi cross) of the 2 F_2 populations were analyzed, with each population representing progeny from 1 broiler grandsire and 1 F_1 sire of each cross.

Phenotypic Measurements

Body weight was measured at hatch and in 2-wk intervals up to 8 wk of age. Average daily weight gain (**ADG**) was calculated as the average daily change in BW between 2 consecutive BW measurements.

Marker Selection and Genotyping

Microsatellite markers from primer kits 1 to 4 were supplied by the Poultry Subcommittee of the National Animal Genome Research Program (USDA, Washington, DC). Using the available marker intervals from the chicken genetic consensus map (http://www.thearkdb.org), markers were selected to test in the parental inbred lines and the broiler (grandsire #360) of the IGCRP. The PCR amplification of 50 ng of genomic DNA from these parental samples with fluorescently labeled primers (either with 6FAM-, HEX-, or TET-) was used to identify markers that would be informative (polymorphic) in the IGCRP. Markers were selected to test based on their position on the consensus map. A target for marker spacing of 10 cM was used to test markers across the genome. If a given marker was informative in the IGCRP, then the next adjacent marker present in the primer kits had to be at least 10 cM away for it to be evaluated for polymorphic content. Any gaps in marker coverage larger than 20 cM were filled by markers identified using the consensus map and synthesized denovo with either a 6FAM- or HEX- fluorescent label. Marker screening and any pilot genotyping were conducted using an ABI310 genetic analyzer (Applied Biosystems, Foster City, CA). The PCR was conducted in 384-well format using an MJ Research-Tetrad thermal cycler (Global Medical Instrumentation, Ramsey, MN). Reactions were setup using a Multiprobe II robotic liquid handler (Packard Instruments Co. Inc., Meriden, CT) in 384-well format from genomic DNA stocks stored in 96-well format. The PCR reaction conditions varied, depending on the marker being genotyped, from 1.5 to 4 m*M* Mg Cl2, 0.1 to 0.25 μ*M* primers, with annealing temperatures from 48 to 64°C. All reactions contained 50 ng of genomic DNA in a total reaction volume of 12 μL.

All IGCRP F_2 genotyping was conducted using an ABI3700 genetic analyzer (Applied Biosystems) by pooling PCR products from 2 markers labeled with different fluorescent dyes. All genotyping with Applied Biosystems instruments utilized the ROX-400HD internal size standard for accurate microsatellite allele sizing. Genotypes were obtained using Genotyper software (Applied Biosystems), and the data were exported to Microsoft Excel (Microsoft Corp., Redmond, WA) for archiving.

Linkage Analysis and QTL Mapping

Marker linkage analysis was performed using CRIMAP program package Version 2.4 (Green et al., 1990). All markers were preprocessed in terms of polymorphism between broiler sire and Leghorn and Fayoumi dam lines and genotype errors. Markers that did not meet these criteria were deleted from analysis. Option FLIPS and ALL were used to get the best order of the markers, and the FIXED option was used to obtain the map distance among markers. The maps were then used for QTL detection on the 18 autosomes, 2 linkage groups, and the Z chromosome by using QTL Express software (Seaton et al., 2002). The least square regression model was used for QTL analysis including the fixed effects of sex and hatch, along with additive and dominance coefficients for the putative QTL. Detection of QTL was based on an F statistic that was computed from sums of squares explained by the additive and dominance coefficients for the QTL. Significance thresholds of the F statistic were derived at the chromosome and genome-wise levels on a single-trait basis by the permutation test. Average thresholds across the 8 traits in each F_2 cross were used for significance

Table 1. Phenotypic correlations between BW and average daily gain (ADG) traits in the F_2 population ($P < 0.05$)

Trait	BW4	BW6	BW8	ADG0-2	ADG2-4	ADG4-6	ADG6-8
BW2	0.86	0.73	0.68	1.00	0.75	0.44	0.50
BW4	—	0.86	0.83	0.86	0.98	0.52	0.65
BW6	—	—	0.95	0.73	0.84	0.89	0.73
BW8	—	—	—	0.68	0.82	0.84	0.92
ADG0-2	—	—	—	—	0.75	0.44	0.49
ADG2-4	—	—	—	—	—	0.51	0.67
ADG4-6	—	—	—	—	—	—	0.62

testing. A total of 5,000 random permutations of the data were performed. The 5% chromosome-wise level threshold was used as suggestive QTL, and the 5% genome-wise level threshold was used as significant QTL. Percentage of F_2 variance explained by model was calculated as

$$\text{variance percentage} = 100 \times (\text{RMS} - \text{FMS})/\text{RMS}$$

where RMS = the residual mean square from the reduced model, omitting QTL but including all fixed effects, and FMS = the residual mean square from the full model, including QTL and all fixed effects.

RESULTS

Phenotypic Correlations Between Growth Traits

The phenotypic correlations between growth traits in the combined 2 F_2 populations are presented in Table 1. In general, there were high positive correlations between each 2 traits, as expected. Phenotypic correlations between any BW traits and neighbor BW traits or average daily gain traits in terms of measuring time were relatively higher than other correlations, such as correlations among BW6 and BW4 (0.86), BW8 (0.95), ADG2-4 (0.84), and ADG4-6 (0.89).

Chromosome Linkage Map

The 269 microsatellite markers genotyped in the 2 F_2 crosses cover 23 autosomes, 3 linkage groups, the Z chromosome, and an unknown linkage group. The chromosomes or linkage groups were eliminated from the linkage analysis if there were less than 3 markers for each chromosome after preprocessing of all the markers. The number of microsatellite markers, chromosome map length, and average marker interval by chromosome in 2 F_2 crosses are presented in Table 2. Ultimately, 19 autosomes, 1 linkage group, and the Z chromosome containing 195 microsatellite markers in the broiler-Leghorn cross were used for linkage analysis. The total map length was 42.77 M, with average spacing of markers of 21.93 cM ranging from 8.71 to 31.33 cM. Nineteen autosomes, 2 linkage groups, and the Z chromosome containing 191 microsatellite markers were used for linkage analysis in the broiler-Fayoumi cross, with total map length of 38.35 morgan. The average marker interval ranges from 6.03 to 28.86 cM with average spacing of markers of 20.08 cM across chromosomes in the broiler-Fayoumi cross. In general, map order of the markers in both F_2 crosses was similar to the chicken consensus map. Map lengths for these chromosomes were considerably longer compared with the chicken consensus map.

Significance Thresholds

Individual chromosome significance levels at the 5 and 1% levels, as determined by the permutation test, differed slightly by trait within chromosome (Table 3). Average 5% chromosome-wise thresholds ranged from 3.99 to 7.03 in the broiler-Leghorn cross and from 4.29 to 7.05 in the broiler-Fayoumi cross. Average 1% chromosome-wise thresholds ranged from 5.75 to 8.97 in the broiler-Leghorn cross and from 6.14 to 8.90 in the broiler-Fayoumi cross. Average 5 and 1% genome-wise thresholds were 9.12 and 11.28, respectively, in the broiler-Leghorn cross and were 9.08 and 11.14, respectively, in the broiler-Fayoumi cross.

General QTL Mapping Results

Estimates for QTL significant at the 5% chromosome-wise level are presented in Tables 4 and 5. For the QTL graphs, representing plots of the F statistic across chromosomes, only QTL significant at the 1% chromosome-wise level are presented in Figure 1, panels A and B, (BW traits) and Figure 2, panels A and B (average daily gain). For comparison purposes, if 1 QTL in a group of traits in 1 cross was significant at the 1% chromosome-wise level, QTL for all traits in the both F_2 crosses were presented. Although some graphs suggest evidence for multiple QTL in adjacent intervals for the same trait, only results for the most significant position were presented in Tables 4 and 5, because only single QTL models were tested.

A total of 52 and 38 QTL were detected at the 5% chromosome-wise level for the 8 traits evaluated in the broiler-Leghorn cross and the broiler-Fayoumi cross, respectively, not counting potential multiple QTL in adjacent intervals. Nine QTL would be expected to be significant at the suggestive threshold by chance alone, given the 8 traits examined. Therefore, over 5 and 4 times as many QTL were detected at this level than were expected by chance in the broiler-Leghorn cross and the broiler-Fayoumi cross, respectively. Of the 52 suggestive QTL in the broiler-Leghorn cross, 17 QTL were significant at the

Table 2. Number of informative microsatellite markers, chromosome (linkage) group map length, and marker intervals

	Broiler-Leghorn cross			Broiler-Fayoumi cross		
Gga	Marker (no.)	Map length (cM)	Average marker interval	Marker (no.)	Map length (cM)	Average marker interval
1	30	836.9	27.9	37	703.7	19.0
2	26	539.4	20.8	29	801.5	27.6
3	21	507.0	24.1	15	432.9	28.9
4	15	470.0	31.3	12	277.2	23.1
5	11	236.8	21.5	10	157.5	15.8
6	10	166.8	16.7	7	122.4	17.5
7	10	243.0	24.3	10	238.5	23.9
8	6	77.4	12.9	5	87.6	17.5
9	9	235.5	26.1	9	125.4	13.9
10	8	156.5	19.6	6	125.9	21.0
11	4	41.8	10.5	5	60.8	12.2
12	4	50.1	12.5	3	55.9	18.6
13	4	56.3	14.1	6	91.9	15.3
14	5	122.4	24.5	3	41.0	13.7
15	6	52.3	8.7	3	27.4	9.1
17	4	102.9	25.7	6	76.9	12.8
18	4	74.4	18.6	3	55.9	18.6
24	3	37.3	12.4	4	88.1	22.0
27	3	72.6	24.2	3	63.0	21.0
E46	3	73.8	24.6	3	82.7	27.6
E47	—	—	—	3	18.1	6.0
Z	9	123.2	13.7	9	100.8	11.2
Total	195	4,277	21.9	191	3,835	20.1

5% genome-wise level (Table 4). Of the 38 suggestive QTL in the broiler-Fayoumi cross, 10 QTL were significant at the 5% genome-wise level (Table 5). Over the 8 traits examined, 1 QTL would be expected to be significant at this level by chance alone. Thus, clearly, more QTL were identified at this level than were expected. In general, the additive effect suggested that broiler alleles were superior (greater weight and faster growth) to both Leghorn and Fayoumi alleles, except for the QTL affecting BW2 and ADG0-2 on Gga 14, QTL affecting BW8 and ADG4-6 on Gga 18 in the broiler-Leghorn cross, and for the QTL affecting BW2 and ADG0-2 on Gga 4 in the broiler-Fayoumi cross (Tables 4 and 5).

There were no QTL affecting growth-related traits detected on chromosomes 11, 12, 13, 15, 17, 27, and Z in the broiler-Leghorn cross, whereas there were no QTL detected on chromosomes 10, 11, 12, 15, 17, 18, 24, 27, E46, E47, and Z in the broiler-Fayoumi cross. The phenotypic trait variances explained by QTL ranged from 2.24 to 10.12% in the broiler-Leghorn cross and from 2.94 to 9.14% in the broiler-Fayoumi cross.

BW2. For the broiler-Leghorn cross, QTL effects on BW at 2 wk were detected on chromosomes 1, 2, 4, 5, 7, 10, 14, and E46 (Table 4). Two of 8 QTL were significant at the 5% genome-wise level (Table 6). Four of the 8 QTL showed overdominance (3 with a high degree of overdominance). For 2 of the 4 QTL, heterozygotes concerning QTL breed origin had lower BW than either of the homozygotes, and the opposite effect was observed for another 2 QTL (Table 4). For the broiler-Fayoumi cross, QTL were identified on chromosomes 1, 2, 4, 5, 6, and 13 (Table 5). Two of 6 QTL were significant at the 5% genome-wise level (Table 6). Two of the 6 QTL showed high degrees of overdominance, and 1 QTL had near complete dominance. Heterozygotes had higher BW at 2 wk than either of the homozygotes in 2 QTL with overdominance effects (Table 5). The total trait variances explained by QTL were 32.12% in broiler-Leghorn and 29.33% in broiler-Fayoumi crosses, respectively (Table 6).

BW4. For the broiler-Leghorn cross, 6 QTL were identified at the 5% chromosome-wise level for BW at 4 wk on Gga 1, 2, 4, 7, 10, and 14 (Table 4). Three of the 6 QTL showed high degrees of overdominance. Heterozygotes had higher BW at 4 wk than either of the homozygotes in 2 of the 3 QTL with overdominance effects (Table 4). For the broiler-Fayoumi cross, QTL were identified on Gga 1, 2, 5, 7, 8, and 13 (Table 5). Three of 6 QTL had overdominance effects. For 2 of the 3 QTL, heterozygotes

Table 3. The 5 and 1% chromosome-wise significance levels, as determined by permutation test, for BW and average daily gain by chromosome in broiler-Leghorn cross and broiler-Fayoumi cross

	Broiler-Leghorn cross		Broiler-Fayoumi cross	
Gga	5%	1%	5%	1%
1	7.0	9.0	7.1	8.9
2	6.7	8.6	7.0	8.8
3	6.4	8.5	6.2	8.0
4	5.7	7.6	5.5	7.5
5	5.6	7.5	5.4	7.5
6	5.0	6.8	5.1	7.2
7	5.3	7.3	5.2	7.1
8	4.6	6.5	4.5	6.3
9	5.3	7.2	5.4	7.3
10	4.9	6.9	—	—
13	—	—	5.4	7.3
14	5.0	6.8	4.3	6.1
18	4.8	6.9	—	—
24	4.2	6.1	—	—
E46	4.0	5.8	—	—

Table 4. The QTL significant at the 5% chromosome-wise level for BW and average daily gain (ADG) in the broiler-Leghorn cross. Estimated significance levels (*F*-value), location, gene effects, and percentage of F_2 variance explained by each QTL.

Gga	Trait	*F*-value	Location	Additive effect[1]	SE	Dominance effect[2]	SE	Variance (%)
1	BW2	7.96	687	7.72	1.95	0.07	2.82	4.38
1	BW4	10.32**	688	29.12	6.55	4.73	9.57	5.59
1	BW6	7.92	0	27.40	13.03	–42.85	16.16	4.35
1	BW8	9.08*	0	49.19	20.23	–67.20	25.10	4.96
1	ADG0-2	8.45	687	0.56	0.14	–0.01	0.198	4.63
1	ADG2-4	9.85**	217	2.04	0.46	0.39	0.66	5.36
1	ADG4-6	7.83	0	1.15	0.51	–1.57	0.63	4.30
1	ADG6-8	7.38	1	1.63	0.65	–1.78	0.83	4.07
2	BW2	12.33***	235	8.26	1.88	–8.89	3.32	6.62
2	BW4	14.66***	241	34.37	6.40	–15.80	11.99	7.77
2	BW6	14.73***	241	62.80	11.58	–17.74	21.68	7.80
2	BW8	12.64***	246	88.94	17.91	3.16	32.46	6.77
2	ADG0-2	11.85***	235	0.57	0.13	–0.61	0.23	6.37
2	ADG2-4	13.9***	243	1.83	0.35	–0.53	0.65	7.40
2	ADG4-6	9.91**	241	2.03	0.46	–0.14	0.86	5.39
2	ADG6-8	7.69	256	1.68	0.50	1.03	0.74	4.23
3	BW6	6.37	134	70.85	23.45	–39.66	32.38	3.53
3	ADG4-6	7.93	109	2.46	0.62	–0.56	0.82	4.36
4	BW2	9.87**	414	12.82	3.03	0.56	5.79	5.37
4	BW4	11.16**	421	38.22	8.67	8.65	14.62	6.03
4	BW6	17.26***	434	78.14	14.40	28.13	23.03	9.03
4	BW8	19.58***	439	141.28	23.91	43.11	41.75	10.12
4	ADG0-2	10.38**	414	0.93	0.21	0.02	0.41	5.63
4	ADG2-4	10.13***	433	1.80	0.43	0.58	0.68	5.50
4	ADG4-6	17.53***	435	3.06	0.57	1.37	0.93	9.15
4	ADG6-8	16.84***	446	4.44	0.79	0.94	1.53	8.83
5	BW2	5.61	101	7.56	2.58	3.73	3.87	3.12
6	ADG0-2	5.02	45	0.69	0.25	0.17	0.32	2.81
7	BW2	5.30	14	4.54	2.26	–10.07	3.49	2.95
7	BW4	6.60	21	15.49	6.53	–27.17	8.73	3.65
7	BW6	6.70	77	54.20	15.64	5.74	23.72	3.71
7	BW8	7.00	75	91.48	24.48	–30.50	36.33	3.87
7	ADG0-2	5.31	13	0.31	0.16	–0.74	0.25	2.96
7	ADG2-4	6.21	22	0.82	0.35	–1.34	0.45	3.45
7	ADG4-6	6.20	76	2.0	0.61	0.37	0.92	3.44
7	ADG6-8	6.46	75	2.63	0.78	–2.39	1.15	3.58
8	ADG6-8	5.68	17	3.18	1.39	–0.39	1.51	3.16
9	BW6	5.45	168	74.05	37.46	–24.87	40.67	3.04
9	BW8	5.63	157	109.46	52.53	–7.54	74.88	3.14
9	ADG4-6	7.33	165	3.44	1.47	–1.17	1.72	4.04
10	BW2	7.35	21	2.32	3.35	12.97	4.70	4.05
10	BW4	6.25	18	8.06	10	38.94	14.61	3.46
10	ADG0-2	7.78	21	0.16	0.24	0.94	0.33	4.27
14	BW2	6.04	91	–0.62	3.65	14.11	4.91	3.35
14	BW4	5.70	95	8.98	12.90	56.67	18.56	3.17
14	ADG0-2	6.14	90	–0.06	0.25	0.97	0.33	3.41
14	ADG6-8	6.68	59	5.55	1.63	3.23	1.75	3.70
18	BW8	4.63	21	–128.56	42.93	–71.09	52.30	2.70
18	ADG4-6	5.14	23	–3.22	1.0	–1.89	1.28	2.87
24	ADG2-4	4.51	0	1.05	0.35	–0.10	0.45	2.53
E46	BW2	4.06	0	7.14	2.55	3.48	5.96	2.28
E46	ADG0-2	3.99	0	0.50	0.18	0.19	0.42	2.24

[1]Additive (a) and dominance (d) QTL effects correspond to genotype values of +a, d, and –a, respectively, for individuals having inherited 2 broiler alleles, heterozygotes, and individuals with 2 inbred alleles. Positive additive effects indicate that broiler alleles associated with high trait values; negative additive effects indicate that broiler allelles associated with low trait values.

[2]Dominance effects are relative to the mean of the 2 homozygotes.

*Significant at 1% chromosome-wise level; **significant at 5% genome-wise level ($F > 9.12$); and ***significant at 1% genome-wise level ($F > 11.28$).

had lower BW at 4 wk than either of the homozygotes (Table 5). The total trait variances explained by QTL were 28.67% in broiler-Leghorn and 29.12% in broiler-Fayoumi crosses, respectively (Table 6).

BW6. For the broiler-Leghorn cross, QTL effects on BW at 6 wk were detected on Gga 1, 2, 3, 4, 7, and 9 (Table 4). One of the 6 QTL showed overdominance with heterozygotes showing the lowest BW at 6 wk. For the broiler-Fayoumi cross, QTL were identified on Gga 1, 2, 3, 4, 8, and 13 (Table 5). Three of the 6 QTL showed strong overdominance. Heterozygotes at QTL on Gga 2 and 13 had the lowest BW at 6 wk. The total trait variances explained by QTL were 31.46% in broiler-Leghorn and 31.56% in broiler-Fayoumi crosses, respectively (Table 6).

Table 5. The QTL significant at the 5% chromosome-wise level for BW and average daily gain (ADG) in the broiler-Fayoumi cross. Estimated significance levels (*F*-value), location, gene effects, and percentage of F_2 variance explained by each QTL.

Gga	Trait	*F*-value	Location	Additive effect[1]	SE	Dominance effect[2]	SE	Variance (%)
1	BW2	7.74	438	7.56	1.93	1.87	2.84	4.99
1	BW4	14.17***	439	32.53	6.53	7.43	9.21	8.76
1	BW6	14.85***	437	55.80	10.28	–0.93	14.74	9.14
1	BW8	12.16***	437	73.51	15.12	–10.43	21.69	7.62
1	ADG0-2	7.52	438	0.52	0.14	0.15	0.20	4.85
1	ADG2-4	14.07***	439	1.78	0.34	0.38	0.50	8.71
1	ADG4-6	10.21**	437	1.75	0.40	–0.56	0.58	6.47
2	BW2	9.1**	468	16.03	4.57	–16.40	5.43	5.81
2	BW4	8.31	465	42.34	14.87	–59.92	18.91	5.34
2	BW6	9.48**	466	81.29	25.69	–107.27	31.93	6.04
2	BW8	8.90*	466	117.10	37.56	–149.65	46.68	5.09
2	ADG0-2	9.21**	468	1.15	0.32	–1.12	0.38	5.88
2	ADG4-6	8.74	64	2.16	0.52	–0.001	0.72	5.59
3	BW6	7.51	323	123.69	48.23	57.07	54.46	4.84
3	ADG4-6	8.24*	325	5.22	2.19	2.37	2.33	5.29
4	BW2	11.05**	241	–5.15	4.20	41.43	9.29	6.97
4	BW6	6.02*	100	48.72	18.79	–0.82	25.15	3.92
4	ADG0-2	11.72***	240	–0.29	0.30	3.00	0.67	7.36
4	ADG4-6	7.27	108	1.81	0.60	1.58	0.81	4.70
5	BW2	5.60	139	11.92	3.77	3.41	3.49	3.66
5	BW4	6.75	89	31.85	10.85	–4.96	13.71	3.75
5	ADG0-2	5.96	139	0.87	0.26	0.27	0.31	3.89
5	ADG4-6	5.63	90	1.69	0.60	–0.24	0.74	3.68
6	BW2	5.20	105	6.88	2.20	–3.24	2.87	3.41
6	ADG2-4	5.19	21	1.14	0.75	–1.67	0.78	3.40
7	BW4	6.58	199	27.74	9.77	–46.16	19.97	4.27
7	ADG2-4	6.81	217	1.72	0.55	–1.58	1.02	4.41
8	BW4	5.40	40	16.26	7.04	25.80	12.32	3.53
8	BW6	5.82	43	21.00	11.51	51.64	19.19	3.79
8	BW8	4.67	41	20.14	17.16	81.72	31.22	3.07
8	ADG2-4	5.53	41	0.84	0.38	1.46	0.45	3.62
8	ADG4-6	4.47	41	0.40	0.44	1.97	0.72	2.94
9	ADG4-6	8.25*	12	2.43	1.37	0.26	1.49	5.29
13	BW2	6.93	58	3.13	3.68	14.02	3.83	4.49
13	BW4	5.30	1	2.72	8.33	–33.02	10.14	3.47
13	BW6	5.88	0	8.64	14.04	–57.38	16.77	3.83
13	ADG0-2	6.63	58	0.20	0.26	0.96	0.27	4.30
14	ADG4-6	4.50	13	3.50	1.33	4.76	1.62	2.96

[1]Additive (a) and dominance (d) QTL effects correspond to genotype values of +a, d, and –a, respectively, for individuals having inherited 2 broiler alleles, heterozygotes, and individuals with 2 inbred alleles. Positive additive effects indicate that broiler alleles associated with high trait values; negative additive effects indicate that broiler allelles associated with low trait values.

[2]Dominance effects are relative to the mean of the 2 homozygotes.

*Significant at 1% chromosome-wise level; **significant at 5% genome-wise level ($F > 9.08$); and ***significant at 1% genome-wise level ($F > 11.14$).

BW8. For the broiler-Leghorn cross, QTL affecting BW at 8 wk were found on chromosome 1, 2, 4, 7, 9, and 18 (Table 4). One of the 6 QTL showed strong overdominance. Heterozygotes showed the lowest BW at 8 wk at QTL on Gga 1. For the broiler-Fayoumi cross, QTL were identified on chromosomes 1, 2, and 8. Two of the 3 QTL showed overdominance effect with opposite effects observed each other. The total trait variances explained by QTL were 31.56% in broiler-Leghorn and 15.78% in broiler-Fayoumi crosses, respectively (Table 6).

ADG0-2. The QTL effects on ADG from 0 to 2 wk were detected on Gga 1, 2, 4, 6, 7, 10, 14, and E46 in the broiler-Leghorn cross (Table 4). Four of the 8 QTL showed overdominance. Heterozygotes had higher ADG0-2 than either of the homozygotes in 2 QTL with overdominance effects (Gga 10 and 14) and lower ADG0-2 on Gga 2 and 7 (Table 4).

Five QTL were identified on chromosomes 1, 2, 4, 5, and 13 in the broiler-Fayoumi cross (Table 5). Two of the 5 QTL showed high degrees of overdominance, and heterozygotes had higher ADG0-2 than either of the homozygotes (Gga 4 and 13, Table 5). The total trait variances explained by QTL were 32.32% in broiler-Leghorn and 26.28% in broiler-Fayoumi crosses, respectively (Table 6).

ADG2-4. Five QTL affecting ADG from 2 to 4 wk were found on Gga 1, 2, 4, 7, and 24 in the broiler-Leghorn cross (Table 4). One of the 5 QTL showed overdominance, and heterozygotes had lower ADG2-4 than either of the homozygotes. Five QTL were identified on chromosomes 1, 6, 7, and 8 in the broiler-Fayoumi cross (Table 5). Two of the 5 QTL showed overdominance, and heterozygotes for the Gga 6 QTL had lower ADG2-4 than either of the homozygotes, with the opposite situation for QTL on Gga

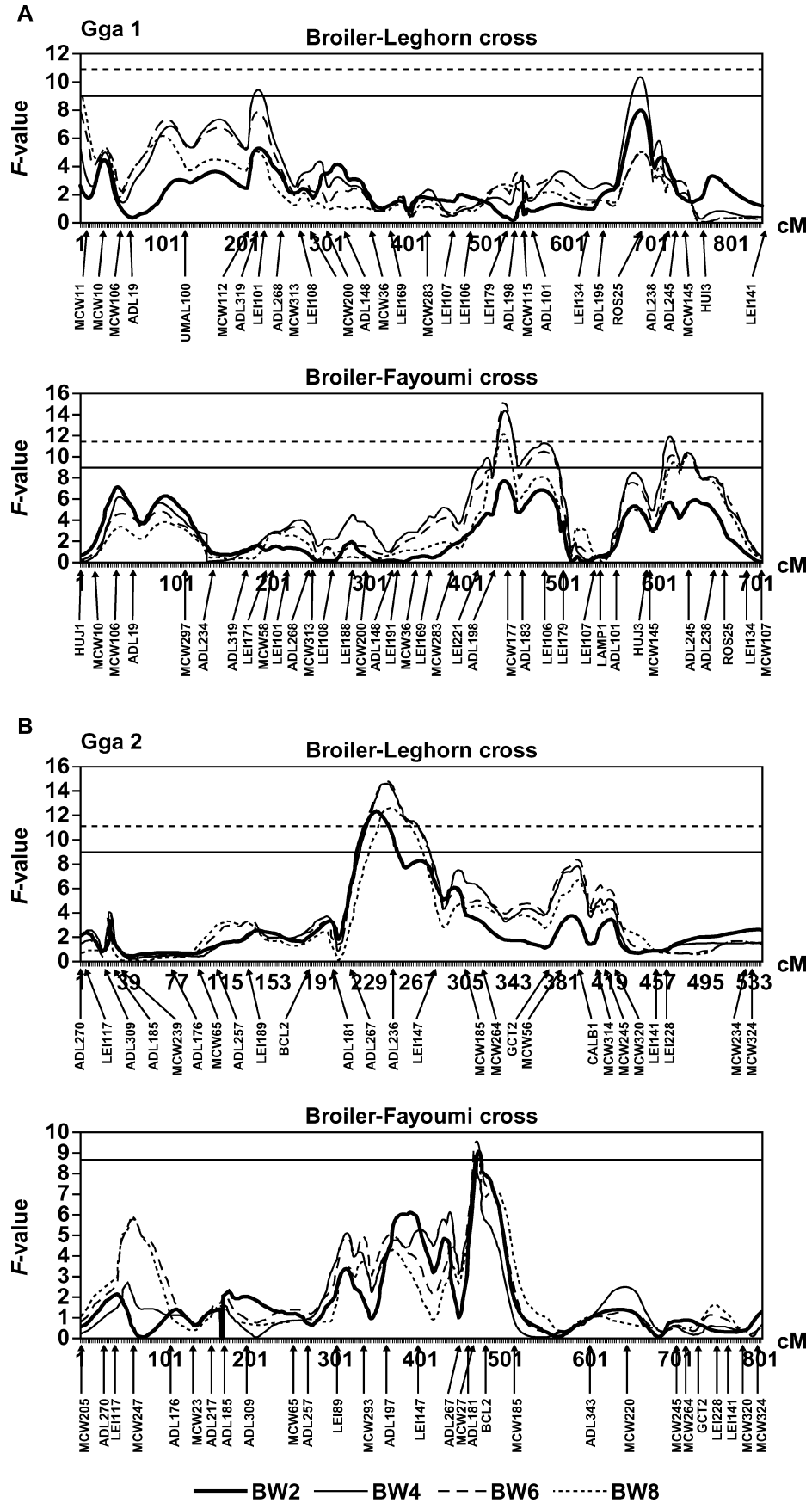

Figure 1. The *F*-value curves for evidence of QTL for BW2, BW4, BW6, and BW8 traits. The x-axis indicates the relative position on the linkage group. The y-axis represents the *F*-value. Arrows on the x-axis indicate the positions in which a marker was present. Two lines are provided for 1% chromosome-wise (----) and 1% genome-wise (—) significance.

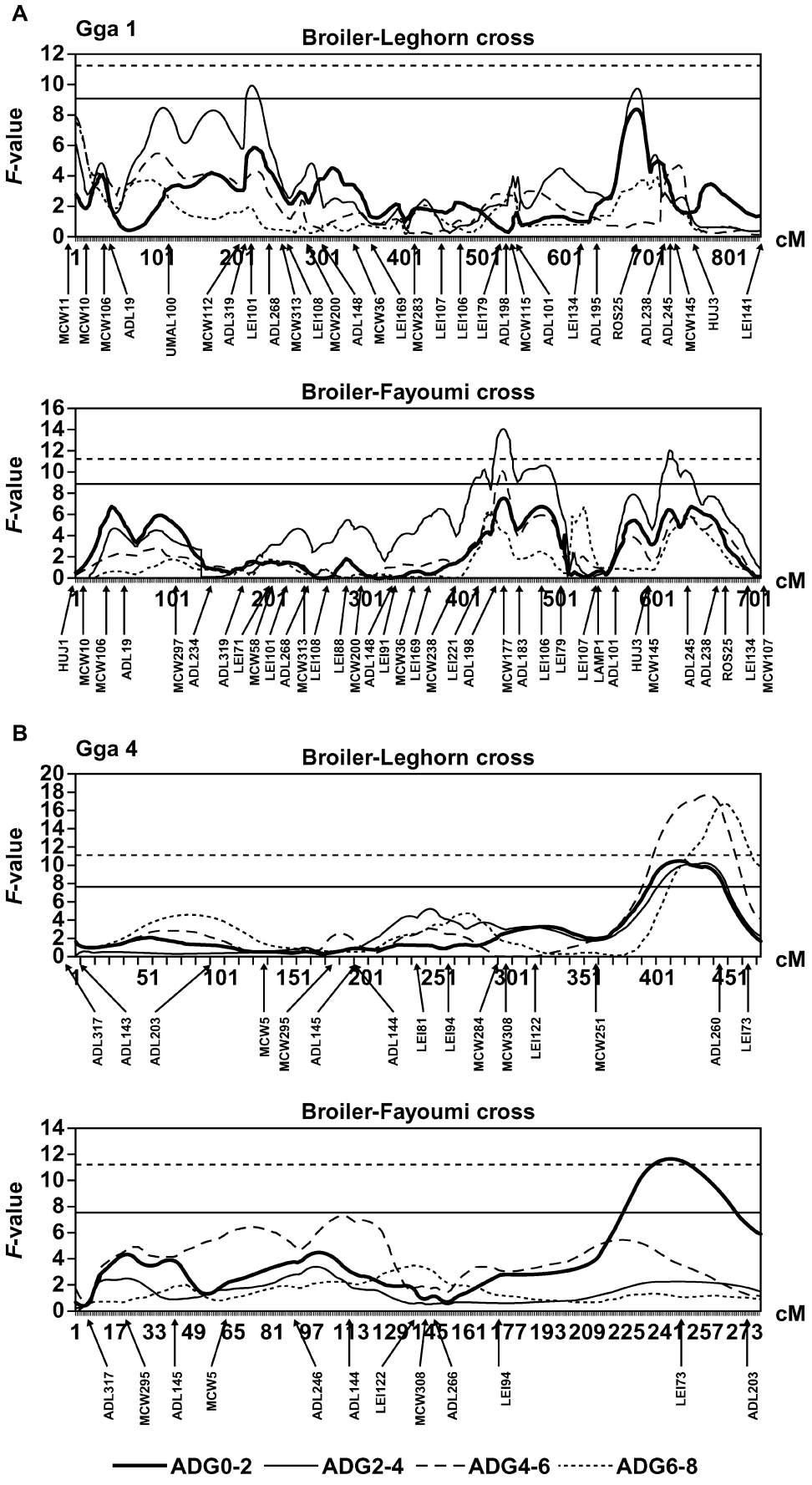

Figure 2. The *F*-value curves for evidence of QTL for average daily gain (ADG) 0-2, ADG2-4, ADG4-6, and ADG6-8 traits. The x-axis indicates the relative position on the linkage group. The y-axis represents the *F*-value. Arrows on the x-axis indicate the positions in which a marker was present. Two lines are provided for 1% chromosome-wise (----) and 1% genome-wise (—) significance.

Table 6. Number of QTL significant at the 5 and 1% chromosome-wise levels (CHR) and genome-wise (GEN) level, by trait in broiler-Leghorn and broiler-Fayoumi F_2 crosses

	Broiler-Leghorn cross					Broiler-Fayoumi cross				
Trait[1]	5% CHR	1% CHR	5% GEN	1% GEN	Variance[2] (%)	5% CHR	1% CHR	5% GEN	1% GEN	Variance[2] (%)
BW2	6	—	1	1	32.1	4	—	2	—	29.3
BW4	3	—	2	1	28.7	5	—	—	1	29.1
BW6	4	—	—	2	31.5	4	—	1	1	31.6
BW8	3	1	—	2	31.6	1	1	—	1	15.8
ADG0-2	6	—	1	1	32.3	3	—	1	1	26.3
ADG2-4	2	—	1	2	24.2	3	—	—	1	20.1
ADG4-6	5	—	1	1	33.6	5	2	1	—	36.9
ADG6-8	5	—	—	1	27.6	—	—	—	—	—

[1]ADG = average daily gain.

[2]The sum of the total variances explained by the individual QTL.

8. The total trait variances explained by QTL were 24.24% in broiler-Leghorn and 20.14% in broiler-Fayoumi crosses, respectively (Table 6).

ADG4-6. The QTL effects on ADG from 4 to 6 wk were detected on Gga 1, 2, 3, 4, 7, 9, and 18 in the broiler-Leghorn cross (Table 4). One of the 7 QTL showed overdominance, and heterozygotes had lower ADG4-6 than either of the homozygotes (Gga 1). Eight QTL were identified on Gga 1, 2, 3, 4, 5, 8, 9, and 14 in the broiler-Fayoumi cross (Table 5). Two of the 8 QTL showed overdominance, and heterozygotes had higher ADG4-6 than either of the homozygotes (Gga 8 and 14). The total trait variances explained by QTL were 33.55% in broiler-Leghorn and 36.92% in broiler-Fayoumi crosses, respectively (Table 6).

ADG6-8. Six QTL, with effects on ADG from 6 to 8 wk, were detected on Gga 1, 2, 4, 7, 8, and 14 in the broiler-Leghorn cross. One of the 6 QTL showed overdominance, and heterozygotes had lower ADG6-8 than either of the homozygotes (Gga 1, Table 4). No QTL were identified in the broiler-Fayoumi cross. The total trait variance explained by QTL was 27.57 in the broiler-Leghorn cross (Table 6).

DISCUSSION

Eight growth traits have been analyzed for QTL detection in the study. The 4 BW traits were actual measurements, whereas the 4 ADG traits were derived from BW and were estimates of the growth rate.

There were similar QTL profiles among the 8 traits within each F_2 cross because of general high correlations among these traits, especially in the traits with very high correlations, such as BW2 and ADG0-2. This suggested that these QTL might have pleiotropic effects on growth at different ages. In contrast, different QTL profiles were observed for the traits with lower correlations, (e.g., BW2 vs. ADG4-6, ADG0-2 vs. ADG4-6).

There were significant differences for all 8 growth traits between the broiler male line and 2 inbred dam lines. The founder line that was initially crossed to generate the F_2 crosses differed extremely in BW at 8 wk, the Leghorn and Fayoumi lines had mean BW of 515 and 492 g, respectively, whereas the broilers had a 3,214-g mean BW (Deeb and Lamont, 2002). The mean BW at 8 wk of the F_2 crosses was 1,575 g for the broiler-Leghorn cross and 1,545 g for the broiler-Fayoumi cross. The BW range was 998 to 2,311 g for the broiler-Leghorn cross and 1,013 to 2,316 g in the broiler-Fayoumi cross. Most of the additive effects detected in the study showed positive value, as expected. However, both inbred lines in the study had a cryptic allele for growth (2-wk BW and ADG0-2 on Gga 14 and 8-wk BW on Gga 18 in the broiler-Leghorn cross; 2-wk BW on Gga 4 in the broiler-Fayoumi cross), whereas the broiler allele was associated with considerably lower growth in these QTL. The cryptic alleles for growth in the current study have been not reported in other studies, although these QTL locations for growth traits were reported in other studies (Sewalem et al., 2002; Carlborg et al., 2003, 2004; Kerje et al., 2003; Jennen et al., 2004). Two reasons might explain these phenomenas: 1) different crosses used in various studies and 2) different ages of measurement of growth among studies. If these cryptic alleles are confirmed in future studies, inbred-line alleles for these QTL can be introgressed as a unique source of alleles into breeding program for improving growth in chickens in the future by MAS.

Many studies have been conducted to detect QTL affecting growth traits in chickens. The F_2 population used in the present study is similar to the QTL study by Sewalem et al. (2002), in which a F_2 population was generated from a commercial broiler line and White Leghorn line. Even though the ages of growth traits in their study were slightly different than the current study, all QTL for growth traits found in their study were detected in the present study, except for QTL on Gga 27 and Gga Z. This independent confirmation of QTL location helps verify the true nature of these QTL. Several QTL detected in the current study were not shown in the study of Sewalem et al. (2002; Gga 3, 10, 14, and 18), and this might be because they did not use these markers in Gga 10, 14, and 18. For QTL on Gga 3, there were few QTL detected for growth, compared with other large chromosomes such as Gga 1, 2, and 4. In this study, 3 out of 4 QTL on Gga 3 were suggestive QTL. McElroy et al. (2006), Carlborg et al. (2003), and Jennen et al. (2004) reported QTL for growth on Gga 3. The QTL for growth on Gga 10, 14, and

Table 7. Positional candidate genes for growth quantitative trait loci (QTL) identified in both the broiler-Leghorn and broiler-Fayoumi crosses

Gga	Location	Line cross	Trait[1]	Positional candidate gene(s)
1	ROS25-ADL238	Leghorn	BW4, ADG2-4	Growth hormone 1
1	ADL183-LEI106	Fayoumi	BW2, BW6, BW8 ADG2-4, ADG4-6	Lysosomal associated membrane protein 1, uncoupling protein 2
2	ADL267-ADL236	Leghorn	BW2, BW4, BW6, BW8, ADG0-2, ADG2-4, ADG4-6	Transforming growth factor-β receptor 1
2	BCL2-MCW185	Fayoumi	BW2, BW6, BW8, ADG0-2	Adenylate cyclase-activating polypeptide 1
4	ADL260-LEI73	Leghorn	BW2, BW4, BW6, BW8, ADG0-2, ADG2-4, ADG4-6, ADG6-8	Transforming growth factor-β type II receptor
		Fayoumi	BW2, ADG0-2	
9	ROS78-ADL136	Fayoumi	ADG4-6	Small inducible cytokine subfamily A
10	ADL158-LEI112	Leghorn	BW2, ADG0-2	Insulin-like growth factor type 1 receptor

[1]ADG = average daily gain.

18 in the present study were also found in a F_3 population crossed by 2 White Plymouth Rock broilers (Jennen et al. 2004) and in a F_2 population generated by Red Jungle Fowl and White Leghorn line (Carlborg et al., 2003). Several QTL for growth traits on Gga 11, 12, and 15 were reported in other studies (Carlborg et al., 2003; Kerje et al., 2003), which were not identified in our study. Carlborg et al. (2003) and McElroy et al. (2006) found QTL for growth on Gga 20 and 26, whereas the current study did not evaluate these 2 chromosomes. The present study identified new QTL for growth traits on Gga 24 and E46 that have not been reported in any other studies.

A strength of the current study was that the conditions for trait recording and the majority of markers were identical across the 2 F_2 crosses. Therefore, line cross-specific effects of QTL could be confidently compared. Despite the similar BW and ADG between 2 inbred parent lines (Leghorn and Fayoumi) and between the 2 F_2 crosses (Deeb and Lamont, 2002), different QTL positions or effects between the 2 different crosses were observed. For example, for BW and ADG traits, both line crosses shared 1 QTL position on Gga 1 (687 cM on the broiler-Leghorn cross and 610 cM on the broiler-Fayoumi cross); however, the 2 line crosses also had unique QTL on Gga 1 for these traits (218 cM on the broiler-Leghorn cross and 439 cM on the broiler-Fayoumi cross). On Gga 4 for 2-wk BW and ADG0-2 traits, similar QTL positions were detected for both line crosses; however, distinct QTL effects were found between the 2 line crosses. The broiler-Leghorn cross had a positive additive effect, as expected for this QTL, whereas the broiler-Fayoumi cross had a negative additive effect, which means that the Fayoumi QTL allele had greater 2-wk BW and ADG0-2 than the broiler QTL allele. Majority QTL detected for growth traits in this study were similar between the 2 line crosses; however, a few QTL showed considerable differences for QTL position and effects between the 2 line crosses. These results suggested that similar phenotypic values for growth traits between the 2 inbred dam lines were not necessarily contributed by same genes with similar effects. The diversity of QTL detected in the 2 different F_2 crosses provides more opportunities to identify genomic regions bearing QTL and, eventually, the causative genes.

The QTL found in the current study generally covered a 20 to 30 cM chromosome region, given the linkage disequilibrium in a F_2 population. This size region will contain many candidate genes. Studies on growth and other growth-related traits in human, mouse, and livestock species provide useful information for identifying potential positional candidate genes. Based on the comparative maps among humans, mice, and chickens, potential candidate genes can be selected for the regions of interest.

In the present study, QTL that had large influences on growth traits were located on several major chromosomal regions (Gga 1, 2, and 4 for the broiler-Leghorn cross and Gga 1, 2, 3, 4, and 9 for the broiler-Fayoumi cross). For Gga 1, potential positional candidate genes are growth hormone 1, lysosomal associated membrane protein 1, and uncoupling protein 2 (Table 7). The potential candidate genes mapped in the region on Gga 2 are transforming growth factor-β (**TGFB**) type I receptor and pituitary adenylate cyclase-activating polypeptide 1. The TGFB type II receptor is mapped on Gga 4 nearby QTL affecting growth traits. A potential candidate gene on Gga 10 is insulin-like growth factor type 1 receptor. Growth hormone gene has been associated with growth in chickens (Kuhn et al., 2002). The insulin-like growth factor and TGFB family genes have previously shown associations with growth-related traits in chickens (Amills et al., 2003; Li et al., 2003; Zhou et al., 2005). In the human, pituitary adenylate cyclase-activating polypeptide 1 has been indicated to increase growth hormone release (Yunker and Chang, 2004). So far, no association has been found for the genes above with growth-related traits in chickens.

The single-QTL model was used to detect QTL for growth-related traits in the current study. Different QTL locations in the same chromosome were observed on several chromosomes, such as Gga 1 and 2. Further analysis with multitrait QTL model might confirm these multiple QTL. The dissection of the underlying mechanism of quantitative traits is very complicated. Carlborg et al. (2004) have used simultaneous mapping method to detect epistatic QTL for growth traits in chickens. This method increased 30% QTL for growth compared with the 1-dimensional method. Further studies with this approach

might be able to obtain more understanding of the complex genetic architecture underlying quantitative trait variation for growth in chickens. The present genome-wide QTL mapping in 2 F_2 populations lays the foundation for identifying the DNA variants causally responsible for variation in growth traits in chickens. To utilize these results for further identifying causative functional genes or using MAS for animal improvement, fine-mapping QTL needs be conducted or segregation of QTL within commercial population needs be verified before further efforts are made. De Koning et al. (2003, 2004) validated the presence of QTL for BW and feed conversion in a commercial broiler line. Confirmation of QTL for fatness in chickens in an advanced intercross line (F_9) was achieved by Jennen (2004). The current development of advanced intercross lines from the current F_2 populations provides an opportunity to further fine-map QTL and positionally map causative genes responsible for the economically important growth-related traits in chickens.

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